and the larger a little beyond middle), posterior tarsi robust, first joint long (second and third joints mutilated in type); tegmina about two and a half times as long as broad, moderately narrowed towards apices, which are rounded, apical areas with the veins reticulate and prominent.

Type, K. katzensteini, Berg.

Allied to Mahanarva, vertex larger and of different shape and structure; posterior margin of pronotum truncate, &c.

Kanaima katzensteini.

Tomaspis katzensteinii, Berg, Hem. Argent. p. 233 (1879).

Hab. Argentina.

XXIII.—On the Characters and Affinities of "Desmalopex" and Pteralopex. By KNUD ANDERSEN.

The Differential Characters of "Desmalopex."

The fruit-bat described by Temminck, fifty-six years ago, as Pteropus leucopterus * has recently, by Miller, been made the type of a distinct genus, Desmalopex +, stated to differ from *Pteropus* by a series of cranial and dental characters. Pteropus leucopterus appears to be rare in collections, the only specimens recorded in literature being the type in the Leyden Museum (slightly immature) and two skins with skulls in the British Museum (adults, one of them described by Gray as " Pteropus chinensis" ‡). I have carefully tested all the differential characters of Desmalopex pointed out by Miller on these three skulls of Desmalopex and the whole British Museum series of skulls of Pteropus, representing

* Temminck, Esq. Zool. pp. 60-61 (1853); type locality unknown, "l'on présume une des îles Philippines."

† Miller, 'Families and Genera of Bats,' p. 60 (29 June, 1907).
‡ Gray, 'Catalogue of Monkeys, Lemurs, and Fruit-eating Bats,' p. 111 (1870). This specimen came to the Museum from Robert Fortune, who, from the spring of 1843 to late in 1845, travelled in the northern provinces of China as a collector to the Horticultural Society of London; hence it was, very naturally, believed by Gray to be from China. But the fact was apparently overlooked that Fortune also made an excursion to Luzon (January to early in March, 1845; see his 'Three Years' Wan-derings in the Northern Provinces of China,' pp. 332-345, 1847). When to this it is added that no species of *Pteropus* is known to occur in China, and that the type of Pt. chinensis differs in no essential characters from the type of Pt. leucopterus, there can be no reasonable doubt that the former was in reality obtained by Fortune during his stay in Luzon.

nearly all species known, and arrived at the conclusion that *Desmalopex* cannot be separated from *Pteropus*. It is fair to add, however, that two or three years ago, when Miller was studying the British Museum collection of bat-skulls for his revision of the genera of bats, the series of *Pteropus* skulls was much less complete than now; since then all the species of *Pteropus* have been worked out for the 'Catalogue of Chiroptera,' and the number of skulls now available for examination is more than four times as large. Miller's opportunities for verifying the supposed differential characters of *Desmalopex* were therefore much less favourable than they would be now.

The characters of *Desmalopex* given by Miller (here printed between inverted commas), and my comments thereon, are these :---

(1) "Like *Pteropus*; but skull with broader rostrum and palate."—In no small number of species of *Pteropus* (e. g. *Pt. nawaiensis, samoënsis, anetianus, pselaphon*, tuberculatus, pilosus, insularis, phæocephalus, lombocensis*; among the larger forms *Pt. melanopogon*) the rostrum is quite as broad as or even broader than in *Pt. leucopterus.*

(2) "Orbits directed slightly more upward."—The orbits of *Pt. leucopterus* are not directed more upward than in certain other species of *Pteropus*, e. g. *Pt. vampyrus* and *qiganteus* †.

* A comparison of the measurements of *Pt. leucopterus* and *pselaphon* is perfectly fair, since the skulls of these two species are precisely of the same size (and indeed so similar also in other respects as to differ only in trivial details). Skulls measured, *Pt. leucopterus*, B.M. 62.1.14.3, and (in parentheses) *Pt. pselaphon*, B.M. 94.7.3.2: gnathion to back of zygomatic process of squamosal 54 mm. (54); zygomatic breadth 38 (37): across postero-external corners of alveoli of m^1-m^1 19 (19); across alveolar borders between p^3 and p^4 15⁻⁶ (15⁻⁸); breadth of palate between inner sides of m^2-m^2 12⁻⁵ (13); between postero-internal corners of p^4-p^4 10⁻⁸ (11⁻²); between p^3-p^3 9.8 (9⁻⁷).

† Measurements, by goniometer, of angle formed by alveolar margin (front of p^3 to back of m^1) and tangent to upper and lower edges of orbit:—*Pt. pselaphon* (B.M. 94.7.3.2) 45°, *Pteralopex atrata* (88.1.5.9; type) 32-33°, *Pt. leucopterus* (62.1.14.3) 25°, *Pt. giganteus leucocephalus* (45.1.8.274; Nepal) 27°.—Miller writes (op. cit. p. 61) that the orbits of *Pteralopex* are "strongly upturned," *i. e.* more so than in "*Desmalopex*," and lays some stress on the supposed three stages of the position of the orbits as marked by *Pteropus* (orbits less upturned), *Desmalopex* (more upturned), and *Pteralopex* (strongly upturned), this being one of his arguments for the alleged intermediate position of *Desmalopex* between *Pteropus* and *Pteralopex*. The true facts are those shown by the measurements given above and verified by an instrument still finer than a goniometer, namely, the eye, that *Pt. leucopterus* does not differ in this respect from *Pt. giganteus*, and that the orbits of *Pteralopex* are even slightly less upturned. Miller's mistake is, however, perfectly The above are the only cranial characters of *Desmalopex* given by Miller; all the other characters (numbers 3-9, infrà) are taken from the dentition.

(3) "Upper incisors subequal, distinctly larger than in *Pteropus*, the cross section of the crown nearly one-third that of canine, the cingulum produced into a noticeable shelf posteriorly."—In *Pt. samoënsis, anetianus, pselaphon, pilosus,* and *tuberculatus* the upper incisors are fully as large as, if not larger than, in *Pt. leucopterus,* and at least in the three last species the cingulum is quite or very nearly as broad as in *Pt. leucopterus*; if there is any difference in the development of the eingulum, in favour of *Pt. leucopterus,* it is certainly infinitesimal.

(4) "Lower incisors very unequal, the crown area of the outer nearly one-half that of canine, that of the iuner scarcely more than one-half [probably a slip for one-fifth] as great."—In a majority of species of *Pteropus* i_2 is about once and a half, twice, or twice and a half the bulk of i_1 , but the contrast in size is in some species much greater, i_2 being sometimes four, five, or six times as stout as i_1 . In *Pt. leucopterus* the disproportion is due chiefly to an increase of i_2 ; the same is the case in *Pt. samoënsis, anetianus, pilosus,* and *tuberculatus,* in which i_2 is from three to four times the bulk of i_1 , in *et al. leucopterus* is combined with a distinct reduction of i_1 , making i_2 varying from four to six times the bulk of i_1 , and thus producing a disproportion even larger than in *Pt. leucopterus*.

(5) "Small upper premolar well developed, not deciduous, its diameter nearly half that of upper incisor, its crown flat."—The vanishing p^1 is a trifle less reduced than usually in *Pteropus*, though the difference is exceedingly small indeed between *Pt. leucopterus* and certain specimens of *Pt. lombocensis*, in which p^1 has the crown slightly but distinctly differentiated from the shaft. Whether p^1 is really persisten in *Pt. leucopterus* is impossible to decide on the available material, it would require a much larger series; all that can be said is that it is present in the only three

excusable; it really looks as if the orbits of *Pteralopex* were more directed upward than in *Pt. leucopterus.* The reason is this:—Owing to the excessively heavy canines of *Pteralopex*, the alveolar border, in the usual position of the skull (lower jaw removed, skull resting on a horizontal plane), is much more ascending in postero-anterior direction than in *Pt. leucopterus*; if, however, the two skulls are kept the one above the other, and with their alveolar borders parallel, it is very easily seen that the orbits are less upturned in *Pteralopex* than in *Pt. leucopterus*.

skulls known, one of which is, however, immature, while the teeth of the two other skulls are not much worn; on the other hand, in all the (seven) skulls I have seen of *Pt. lombocensis* p^{1} is present, though some of these skulls have much-worn teeth. It is quite common to find this rudimentary tooth persistent even in aged specimens of *Pteropus*.

(6) "Small lower premolar relatively larger than in *Pteropus*, but smaller than in *Pteralopex*, its outer edge raised but not distinctly cuspidate."—It is a general rule in *Pteropus* that an increase in the size of i_2 is accompanied by an increase in the size of p_1 ; compare, for instance, *Pt. lombocensis*, sameënsis, anetianus, pselaphon, pilosus, tuberculatus. *Pt. leucopterus* follows the same rule (as does also *Pteralopex*), and p_1 is not relatively larger in *Pt. leucopterus* than in *Pt. lombocensis*, sameënsis, anetianus, and pilosus. In structure it does not differ from the typical Pteropine p_1 .

(7) " pm_3 shows no trace of cusp on inner side."—As well known, the structure of a typical Pteropine molar is this: a longitudinal groove flanked by higher outer and lower inner ridge. But in the anterior large premolar above and below (p^3 and p_3) the outer ridge takes more the form of a high acutely pointed cusp, the inner ridge of a lower pointed cusp, and both are anteriorly closely approximated, sometimes completely fused. A fusion of the outer and inner cusps, perfectly similar to that seen in p_3 of *Pt. leucopterus*, is shown by a considerable number of species of *Pteropus*, and in some species, e. g. *Pt. papuanus*, scapulatus, and woodfordi, the fusion of the cusps is decidedly more complete than in *Pt. leucopterus*.

(8) "Molars, both above and below, subquadrate in outline, the length of the crown never conspicuously greater than the width $(m_3 [obviously a misprint for m_1]$ and m¹ not elongated as in Pteropus)."-In species of Pteropus with perfectly unmodified dentition the molariform teeth, particularly m¹, are conspicuously longer than broad; in Pt. leucepterus they are only one-fourth or one-third longer than broad; expressed in other words, they are shorter but not narrower than usual. It is quite natural that this peculiarly shortened form of the cheek-teeth of Pt. leucopterus attracted the attention of Mr. Miller; it is, in fact, not precisely matched by any other Pteropus. But Pt. leucopterus is in this respect approached by Pt. insularis, phaocephalus, macrotis, epularius, poliocephalus, papuanus, and neohibernicus, in all of which the molariform teeth are shorter than usual. And a modification of the outline of the cheek-teeth much greater than that shown by Pt. leucopterus is found in Pt. personatus, scapulatus and woodfordi, in which the teeth are not only much shortened but excessively narrow, as in the Macroglossi. It would be hopeless to "split" the genus *Pteropus* on differences in the general outline of the check-teeth; all modifications lead through numerous transitional stages back to the typical Pteropine molar.

(9) "Lower molars peculiar in that the ridges of m_1 and m_2 are each divided into two low but distinct rounded cusps. The quadritubercular form resulting from this is very noticeable in m₁, less so in m₂."-I am probably not mistaken when I consider this to be, from Miller's point of view, the chief character of his "Desmalopex." It will be necessary, therefore, to make sure if Pt. leucopterus is not, perhaps, in this respect as in all others very closely connected with other species of the genus. In the type of "Pteropus chinensis" (=leucopterus) there is a shallow but distinct transverse depression in the outer and inner ridge of m₁, indicating a beginning subdivision of each ridge into two incompletely differentiated rounded tubercles; the depression is still shallower in the outer than in the inner ridge; in m2 it is, in both ridges, exceedingly shallow, the "quadritubercular" structure of the tooth therefore only detectable on very close examination. In the other skull of Pteropus leucopterus (62.1.14.3) I fail to discover the slightest trace of a depression in the outer ridge of m₁, while in the inner ridge it is present, though less distinct than in the other skull; in m₂ a slight depression is present in the inner ridge and barely detectable (at least with a lens) in the outer ridge. It should be noted that in both skulls the depression is more distinct in m₁ than in m₂, and more distinct in the inner than in the outer ridge. In all the skulls I have seen of Pt. pselaphon (ten) the "splitting" of the inner ridge of m_1 is either as distinct as or (in some skulls) decidedly more distinct than in Pt. leucopterus, and a similar, but much stronger, splitting of the inner ridge is seen in p_4 ; the inner ridge of m_2 is simple, as are also the outer ridges in all teeth. On close examination of a few skulls of Pt. samoënsis and one of Pt. pilosus I find a faint depression in the inner ridge of p4, corresponding in position to the deep groove in p_4 of *Pt. pselaphon*. We have thus these four progressive stages : a majority of species of Pteropus, ridges of lower molariform teeth simple; Pt. samoënsis and pilosus, a slight depression in inner ridge of p₄, suggesting an initial stage towards a splitting of the ridge into two tubercles; Pt. pselaphon, inner ridges of p4 and m1 very distinctly subdivided into an anterior and posterior Ann. & Mag. N. Hist. Ser. 8. Vol. iii. 15

portion; *Pt. leucopterus*, distinct depression in inner ridges of m_1 and m_2 , and, at least sometimes, in outer ridges of same teeth. When to this it is added that *Pt. pilosus* (Pelew Islands), which in this respect marks an intermediate stage between the typical Pteropine dentition and that of *Pt. pselaphon* (Bonin Islands), is the elosest known relative of *Pt. pselaphon*, then the evidence seems to me conclusive. This more or less incomplete, or, if preferred, more or less complete, splitting of the longitudinal ridges of certain cheek-teeth may be used as a specific character (though even as such it is not of much practical use), but it is certainly not of generic importance.

Conclusions .- Pt. leucopterus accords with the typical * species of the Pt. pselaphon group (Pt. pselaphon, pilosus, tuber*culatus*) in the following characters: -(1) The general shape of the skull; (2) the broad rostrum; (3) the strong supraorbital processes; (4) the heavy premaxillæ; (5) the large upper incisors; (6) the unusually broad cingulum of the upper incisors; (7) the enlargement of i_2 ; (8) the heavy eanines, with unusually broad eingulum, the edge of which shows a pronounced tendency to split into separate rounded tubereles; (9) the large p_1 ; (10) the heavy posterior basal ledges of the molariform teeth above and below; (11) the tendency to a splitting of the ridges of some of the lower cheek-teeth; (12) the distribution of the fur (tibiæ densely clothed above); (13) the size and form of the ears; (14) the general size of the animal. The only noteworthy peculiar characters of Pt. leucopterus are, in fact, the shortening of the check-teeth (in which respect it is, however, approached by Pt. insularis and pheocephaius, both allied to Pt. pselaphon) and perhaps the paler colour of the fur (the three specimens known are faded). In the face of this evidence I have not the slightest hesitation in saving that Pt. leucopterus. far from constituting a distinct genus, is simply a Philippine representative of the Pt. pselaphon group. Pt. pselaphon inhabits the Bonin Islands, Pt. pilosus the Pelew Islands, the habitat of Pt. tuberculatus is unknown, but may, not unlikely, be the Mariannes, so that also the geography is in favour of this conclusion.

The Affinities of Pteralopex.

Desmaloper, Miller writes (t. c. p. 60), "is intermediate between *Pteropus* and *Pteraloper*, though nearer the former. In the broadened rostrum and slightly upturned orbits the skull distinctly suggests *Pteraloper*, while the same tendency

* I consider *Pt. insularis* (Ruck atoll, Carolines) and *Pt. phæocephalus* (Mortlock, Carolines) somewhat aberrant members of the *Pt. pselaphon* group.

is shown by the form and relative size of the incisors, the well-developed small upper premolar ["upper" a slip for lower?], the squarish outline of the molars, and the extra cusps of m_1 and m_2 ."

In the foregoing pages I have endeavoured to show that "Desmaloper," i. e. Pt. leucopterus, cannot be separated from Pteropus. But I perfectly agree with Miller that Pt. leucopterus in certain respects distinctly foreshadows Pteraloper, only I must add that this is the case also with the other typical members of the Pt. pselaphon group, viz. Pt. pselaphon, pilosus, and tuberculatus, and that this group is again closely connected with the Pt. samoënsis group (Pt. nawaiensis, samoënsis, anetianus). The following review of all the essential characters of Pteralopex will, I think, place these suggestions as to a rather close relationship between Pteralopex and the Pteropus pselaphon group on a firmer basis :--

(1) General shape of skull Pteropine, on the whole nearest that of the short, broad-faced, heavily-built, strongly-crested skulls of *Pt. pselaphon*, *pilosus*, and *tuberculatus*.

(2) Rostrum short and very broad. In both characters rather closely approached by all species of the *Pt. pselaphon* and *samoënsis* groups, but the rostrum of *Pteralopex* is relatively broader anteriorly, no doubt owing to the excessively heavy upper canines.

(3) Premaxillæ heavy, as in all species of the *Pt. pselaphon* group.

(4) Postorbital processes of frontals strong at base, very long, quite or nearly reaching zygoma; postorbital processes of zygoma small. In all species of the *Pt. pselaphon* group the upper postorbital processes are heavy at base and very long, the lower processes small or practically undeveloped; if, as is the case generally in *Pt. leucopterus* and occasionally in *Pt. pselaphon*, the orbital ring is complete behind, it is therefore formed almost entirely by the upper processes, as in *Pteralopex*.

(5) Coronoid process of mandible high, very broad, steeply ascending (front margin almost at right angles with alveolar border), angular process unusually prominent, rami deep, gonys low (vertical extent), broad, and more steeply ascending than usual. Precisely all the same characters are found in the mandibles of *Pt. pselaphon, pilosus*, and *tuberculatus*; the mandible of *Pt. leucopterus* is weaker, coronoid more sloping, angular process less developed, gonys more typical Pteropine.

(6) Upper incisors very large. The nearest approximation to this in the genus *Pteropus* is found in the species of the *Pt. pselaphon* group.

(7) Cingulum of upper incisors very broad. As in Pt. pselaphon, tuberculatus, and leucopterus.

(8) Great enlargement of i_2 combined with some reduction of i₁, making the contrast in the sizes of these two teeth greater than in any Pteropus. A disproportion between i2 and i₁ is seen already in Boneia, a genus closely allied to the primitive Rousettus; the character is further developed in Pteropus (which no doubt originates from a Rousettus-like form), either by an increase of i_2 or by this combined with a reduction of i₁; and the reduction of i₁ culminates in the complete disappearance of this tooth in Styloctenium and Dobsonia (both genera allied to Pteropus). This character of *Pteraloyex* is therefore only an excessive development of a tendency already present in all the related genera. The numerous species of Pteropus show all intermediate stages, from an i₂ which is only about once and a half the bulk of i_1 , to an i_2 about six times the size of i_1 . The nearest approximation to the enormous disproportion of these teeth exhibited by Pteralopex is seen in the species of the Pt. pselaphon, samoënsis, and lombocensis groups.

(9) Upper canines peculiar in the following points :— (a) cingulum very strongly developed, its edge split into separate tubercles; the same is the case in *Pt. pselaphon*, *pilosus*, and *tuberculatus*, less distinctly in *Pt. leucopterus*; the tubercles of the cingulum in *Pt. pilosus* exactly correspond in number and position to those of *Pteralopex*, only they are slightly smaller: (b) a strong secondary cusp halfway up the hinder edge of the canine; the only species of *Pteropus* possessing a secondary cusp in the upper canines is *Pt. tuberculatus* (of the *pselaphon* group); the cusp in this species is much smaller than, but similar in position to, that of *Pteralopex*.

(10) Cingulum of lower canines broad, forming a conspicuous shelf posteriorly. As in the *Pt. pselaphon* group.

(11) p^3 , p^4 , and m^1 modified as follows:—(a) crown short and broad, subsquarish in outline: (b) hinder (transverse) border of teeth conspicuously raised, front border similarly raised: (c) owing to the shortening of the teeth and the sharply raised anterior and posterior borders, the usual "longitudinal ridges" of a *Pteropus* molar are become much shortened (in antero-posterior extent) so as to form two pointed cusps situated opposite each other, the one on the labial, the other on the lingual side of the tooth, a little in front of the middle. The structure of the *Pteralopex* molar is very easily derived from the molar structure of any species of *Pteropus*, but it is most likely, of course, that it has originated from a tooth in which already the posterior basal ledge (posterior

border) was more developed than usual. Such is the case in the Pt. pselaphon group (as well as in the related Pt. samoënsis group), and in Pt. pselaphon and allied species also the anterior border (cingulum) of p³ and p⁴ is distinctly raised, particularly in p³. Of the four known typical species of the pselaphon group, Pt. leucopterus shows decidedly the nearest approximation to Pteralopex in the general aspect of the upper cheek-teeth; the crown is so much shortened as to be nearly subsquarish, the anterior and posterior borders of each tooth slightly but quite distinctly raised, and the "longitudinal ridges" more shortened and cusp-like than usual. The only additional modifications required to transform an upper molar of Pt. leucopterus into that of a Pteralopear is a further emphasizing of the changes which already have taken place in the passage from a typical Pteropus molar to that of a Pt. leucopterus, viz. a slight further shortening and broadening of the tooth and a much stronger development of the anterior and posterior borders. The difference in this respect between Pt. leucopterus and Pteralopex is unquestionably only one of degree.

(12) p_4 , m_1 , and m_2 modified as follows :-(a) crown shortened and broadened, though not quite to the same degree as in the upper teeth : (b) inner cusp unmodified (not divided), outer cusp bifid (i. e. the tip of the originally simple cusp divided into two cusps by a rather deep groove, which, however, is more conspicuous and goes deeper down on the inner than the outer side of the ridge) : (c) posterior basal ledge very strong, peculiarly oblique, being much more developed on inner than onter side of teeth ; anterior basal ledge undeveloped as in Pteropus generally. All characters much less developed in m₂ than in p₄ and m₁.-A beginning splitting of the ridges (cusps) of the lower cheek-teeth is already seen in Pt. pselaphon and leucopterus (see suprà). In Pt. pselaphon the character is even strongly pronounced in the inner ridge of p_4 , very distinct also in that of m_1 ; in Pt. leucopterus it is distinct in the inner ridges of m, and m_2 , less so, or occasionally scarcely detectable, in the outer ridges of the same teeth. The still stronger splitting of the outer ridges of p4 and m1 of Pteralopex is therefore only a further development of the tendency already well pronounced in Pt. pselaphon and leucopterus. But one difference should be noticed; whenever these characters and tendencies are present in the Pt. pselaphon group, they are either entirely restricted to the inner cusp of the lower cheek-teeth or at least more prouounced in the inner than in the outer cusp; but in Pteralopex the character is, so to say, shifted from the inner cusp, which is absolutely undivided, to the outer

cusp.—Viewed in profile, p_4 , m_1 , and (much less so) m_2 of *Pteralopex* present three cusps behind each other, viz. two higher anterior (the bifd outer cusp) and a low posterior. *This latter is not a cusp peculiar to Pteralopex*; it is homologous to the postero-external cusp arising from the posterior basal ledge in all species of *Pteropus* which have this ledge conspicuously developed.

(13) Distribution of fur (tibiæ densely clothed above). In all details perfectly as in the species of the *Pt. pselaphon* and *samoensis* groups.

(14) Lateral membranes arising, not from the sides of the back, but from the spinal line. There is no parallel to this in any known species of *Pteropus* (but an approximation in *Pt. melanopogon, papuanus*, and *neohibernicus*, in which the membranes arise closer together on the spinal tract than in other *Pteropi*; the character has, however, probably no great taxonomic value, since *Pt. papuanus* and *neohibernicus* belong to a group of species very different from that of which *Pt. melanopogon* is a representative, while, on the other hand, in *Pt. aruensis* and *keyensis*, though both closely allied to *Pt. melanopogon*, the position of the membranes is perfectly normal). An exact parallel is shown by *Dobsonia*, an aberrant genus of the *Pteropus* group.

(15) Ears small, hidden in the fur, so broad above as to be semicircularly rounded off. The cars are small in all species of the *Pt. pselaphon* and *samoēnsis* groups, often hidden in the fur, but in all species more or less narrowly rounded off above. In one single species of *Pteropus* (*Pt. livingstouii*) the ears are very similar in shape to those of *Pteralopex*.

(16) Colour of fur (blackish above and beneath). As in *Pt. pselaphon.*

(17) Size of animal. As an average species of the Pt. pselaphon and samoënsis groups.

Summary.—All the cranial and dental characters of Pteralopex, without any exception, point back to the species of the Pt. pselophon group, much more decidedly than to any other known bats; all external characters, except the insertion of the membranes and the shape of the ears, point in the same direction. From this evidence it appears safe to assume that Pteralopex (Solomon Islands) is a highly specialized offshoot from that branch of Pteropus which in the Bonin Islands, Pelew Islands, Vanikoro (or Mariannes), and Philippines has developed into, respectively, Pt. pselaphon, pilosus, tuberculatus, and leucopterus, and in the Carolines into Pt. insularis and phæocephalus. Also the habitat of Pteralopex is in favour of this conclusion.